

Anatomical Notes on the Mactrid Bivalve,  
*Raeta plicatella* LAMARCK, 1818,  
with  
A Review of the Genus *Raeta* and Related Genera

BY

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(20 Text figures)

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characters which heighten interest about its enigmatic ecology and systematic relationships.

*Raeta plicatella* is the type of its genus. I have therefore included a review of this genus and related ones. Since nothing is known of the anatomies of any of the species of the other genera, conclusions on the systematics of this group must be based on characters of the shell. Description of the shell of *R. plicatella* is deferred to the systematic part of the paper.

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INTRODUCTION

SEVENTY YEARS AGO, DALL (1898, p. 907) wrote of this species:

"Notwithstanding the fact that dead valves of this shell are found in windrows on the beaches at some points of the southern coast, the character of the soft parts is unknown, and I shall be very greatly obliged to any one who can furnish me with a specimen of the animal in spirits in order that its systematic position may be positively settled."

Apparently nothing has yet been reported on its anatomy. It may, therefore, be worth recording notes which I made on a single intact live specimen, and fragments of two others, for this species has several unusual structural

PART I. *Raeta plicatella* (LAMARCK, 1818)

Ecology:

Single, fresh valves are often abundant on the beaches along the Gulf of Mexico in Louisiana and Texas. Very rarely shells have a bored hole, probably made by *Polinices duplicata* SAY, 1822. Joined valves of *Raeta plicatella* are rare and live specimens even more so. I have found only two shells containing the flesh on the beach. Both were at the edge of the surf, and both had been picked open on the central part of the disk by sea gulls. Birds may account for the dearth of live specimens, even in the winter when rough surf often tosses up live snails and bivalves whose shells afford them more protection

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(*Anadara*, *Noctia*, *Dosinia*, *Tellina alternata* SAY, 1822, *Busycon*, *Polinices* and others).

*Raeta plicatella* seems to be a species of the outer part of the surf zone, a region difficult to sample. The mollusks which live there are chiefly known by being cast up on the beach by rough surf, for they are not regularly found in the inner part of the surf zone frequented by swimmers, and several of them are not taken by dredging in waters seaward of this zone. At Galveston, the outer surf zone is only a few hundred yards wide, and from 2 to 3 fathoms depth. It is so close to shore that boats large enough for trawling and dredging cannot often be used there. In more than 60 dredged samples from 3 to 18 fathoms off Galveston, single, small juveniles of *R. plicatella* occurred in two samples at 3 fathoms, and single fragments of larger shells were found in two samples of 5 fathoms. Not even identifiable pieces of shell occurred in any of the others.

I had never seen shell fragments or juveniles of this species in the Galveston Bay complex, until the single intact specimen was found which furnished most of the anatomical data of this report. It was dredged from 2 fathoms, 14 October 1967, at the east end of the intra-coastal canal cutting Pelican Island, Lower Galveston Bay.

Occasional live specimens of mollusks living in the outer surf zone are found in Galveston Bay. These are usually juveniles, or rarely small adults. Their scarcity and size suggest that their larvae have invaded this area, which is adjacent and connected by water to that in which they normally live, but that they are not able to complete their life cycle and establish perpetuating populations in the bays. Examples of such adventitious species found in the more saline parts of the bays, but with established populations only along the Gulf shore are *Dosinia discus* REEVE, 1850, *Tellina alternata* SAY, 1822, *Anadara brasili-ana*, *Periploma inequalis* C. B. ADAMS, 1842, *Noetia ponderosa* SAY, 1822, *Pitar texasiana* DALL, 1889, and *Donax variabilis* SAY, 1822.

#### Behavior:

In the laboratory, the live specimen was lethargic. It did not move about in a dish of seawater, and the foot was not seen extended beyond the shell. The shell gaped slightly and continuously during the several days of observation. The siphons were not withdrawn, even when the specimen was handled.

Several colonies of the stalked ciliate protozoan, *Carchesium*, were attached to the siphons near their tips, and also found on the periostracum between the margins of the valves along the postdorsal slope of the shell. A small colony of an encrusting bryozoan was on the

periostracum of the fused mantle margin near the pedal opening. The surface of the shell was clean and had no extraneous organisms. The presence of *Carchesium* and the bryozoan suggest this animal did not burrow, but was on its side on the substrate. This inference is further supported by the nature of the foot (see below).

#### External Anatomy:

The siphons (slightly contracted in Figure 1) are about  $\frac{2}{3}$  as long as the shell, and joined throughout their length. There is a slight groove between the two, on the sides.

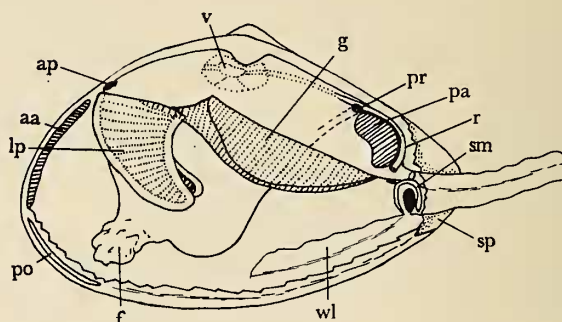


Figure 1

Diagram of the external anatomy of *Raeta plicatella* from a live, partly retracted specimen. The left valve and mantle have been removed.

aa - anterior adductor muscle    ap - anterior pedal retractor muscle  
f - foot    g - gill    lp - labial palp    pa - posterior adductor  
po - pedal opening in mantle margin    pr - posterior pedal retractor  
r - rectum    sm - siphonal membrane    sp - siphonal pocket  
wl - right wall lamella of waste canal    v - ventricle of heart

The diameter of the excurrent siphon is about  $\frac{1}{3}$  that of the incurrent one. The opening of the excurrent siphon has a thin, transparent, conical flange extending from it, with a small opening at its tip. There are no papillae around the excurrent siphonal tip. The incurrent opening has no valve flange, but numerous short papillae are along its margin. Two papillae of this series, between the two siphonal openings, are larger than the rest. Every 10 minutes or so the siphons contracted rapidly, but only for a short distance, and the feces were expelled through the excurrent opening.

A white, wavy seam on the top and bottom of the siphons evidently represents the junction of the two sides of the periostracum. This cuticular sheet extends to the

tips of the siphons, lines the siphonal retraction cavity of the mantle, and all of the exposed mantle margin. It is very thin, and scarcely evident over the outer shell surface.

The color of the living tissue was varied. There was no gross evidence of hemoglobin, the blood being colorless and the nerve ganglia white. The ovary was white, the liver the usual olive brown, the kidney was faint purplish brown. The labial palps and gills were faint orange yellow, and the foot was dingy white. The rest of the flesh was without notable color.

The mantle is very thin, and colorless over the disk of the shell. The disk part is attached in small round spots, which are not the origin of muscle cells, but seem to be epithelial. The spots of attachment are 1 to 2 mm in diameter, and widely scattered.

The kidney extends into the lobes of the mantle, extending downward well below the free margin of the gills (dashed line, Figure 2). This part of the mantle is thickened.

The margins of the mantle lobes are fused to each other along the dorsal, anterior and ventral margins of the shell, and the attachment is thick and muscular. At the antero-ventral margin there is a small opening in the

marginal fusion, the pedal opening (Figure 1). This is surrounded on its inner margin by a thin, narrow velum, which may represent the inner mantle margin lamella. The latter is not evident as a distinct entity elsewhere. No "fourth pallial aperture", below the siphonal pocket, was evident (see YONGE, 1948). At the hind angle of the shell, there is a large opening into the deep, blind siphonal pocket (Figure 1).

In front of the siphonal pocket, the siphonal retractor muscles form a flat, triangular mass in each mantle lobe, with the apex pointing forward. These muscles are small bundles, not forming a continuous sheet, but with spaces between them about half as wide as each bundle (Figure 2, rms). The origin of the siphonal retractor muscles is along the pallial sinus scar of the shell. They converge toward and extend into the siphons as longitudinal retractors.

A thin, transparent diaphragm of mantle epithelium extends forward horizontally from between the inner openings of the siphons. This septum is a continuation of the diaphragm formed by the gill attachments, and with the latter it completely separates the incurrent and excurrent chambers of the mantle cavity (Figure 2, s).

There is a single lamella of mantle extending along both sides and the top of the incurrent siphonal opening, but not across its bottom (Figure 2, sm). This is the siphonal membrane (KELLOGG, 1915). A pair of lamellae of moderate width extend forward from the ends of the siphonal membrane, one attached to each mantle lobe, to a point below the apex of the pallial sinus scar (Figure 1, wl). These are the wall lamellae of the waste canal (KELLOGG, *op. cit.*). These three lamellae have intrinsic musculature, which on contraction decreases the height of the lamellae. They probably serve to guide pseudofeces into the incurrent siphon.

The fused edge of the two mantle lobes ventrally is very thick (Figure 3), and filled chiefly with mantle margin muscles. Some of these pass from the position of the pallial line to the free, or exposed mantle margin, and thus pull the mantle margin upwards, away from the margin of the shell. But the bulk of the muscles pass transversely, forming a mantle margin adductor muscle in this area, as in certain pholads, such as *Cyrtopleura costata*. There are a few strands of longitudinal muscles in this fused mass, particularly on the upper surface.

The periostracum covering the free, ventral surface of the fused mantle margin has a white streak medially. Just above this streak are the two minute grooves (Figure 3, pg) in which the periostracum is formed, between what is homologous to the outer and middle mantle margin lamellae of other bivalves, which do not have fused mantle lobes in this region.

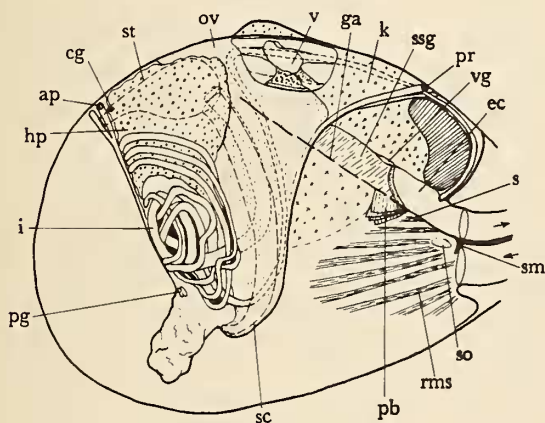


Figure 2

Visceral mass and structures in the mantle at the hind end of the body.

- |   |                                       |
|---|---------------------------------------|
| ap - anterior pedal retractor muscle    | cg - cerebral ganglion                |
| ec - excurrent chamber of mantle cavity | ga - gill axis                        |
| i - intestine                           | hp - liver                            |
| k - kidney                              | ov - ovary                            |
| pg - pedal ganglion                     | pr - posterior pedal retractor muscle |
| rms - retractor muscles of siphons      | sc - style sac                        |
| s - septum separating mantle chambers   | sm - siphonal membrane                |
| so - sense organ                        | ssg - suspensory septum of gills      |
| st - stomach                            | v - ventricle of heart                |
| vg - visceral ganglion                  |                                       |



The anterior adductor muscle (Figure 1, aa) is very elongate and narrow, extending along the anterior curve of the shell from the front end of the pedal opening to the front end of the hinge plate. It is merely a broadening of the mantle margin adductor muscle, and not a separate entity. The hind adductor muscle is reniform, and small for the size of the shell. Both muscles were opaque and white, with no gross evidence of "quick" and "catch" parts differentiated.

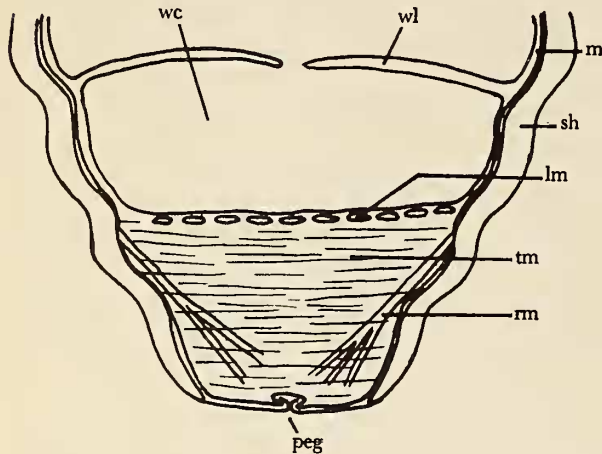


Figure 3

Diagram of transverse section of ventral margin of *Raeta plicatella*, about one fourth the length from the hind end.

lm - longitudinal muscle of mantle margin    m - mantle lobe  
 peg - periostacal groove    rm - retractor muscle of mantle margin  
 sh - shell    tm - transverse muscle of mantle margin  
 wc - waste canal    wl - wall lamella

The foot is atrophied to a small, elongated, wrinkled mass, flattened laterally and rounded at the free end. The free margin is acutely keeled, but without any groove. Probably the foot is never extended beyond the shell margin in specimens of this size (44 mm long). It is somewhat muscular, the circular muscles extending only a little way up on the front margin of the visceral mass, but not up the hind margin of it. Anterior and posterior pedal retractor muscles each form a thin bundle along the front and hind margin, respectively, of the visceral mass (Figure 2, ap, pr). At their top, each muscle divides, the front one originating on the shell valves on each side and slightly above the mouth, and thus just above the anterior adductor muscle. The hind pedal retractor has the rectum passing between its two short branches.

It originates on the shell valves just above the posterior adductor muscle scars.

The visceral mass has an exceptionally thin wall, with little musculature. Probably this is a consequence of the atrophied foot. The covering is so thin that the internal organs of the visceral mass are easily seen through it.

The gills have two demibranchs on each side. The ascending lamellae of all four demibranchs are attached to the mantle at about the level of the gill axes. The gill axes form almost a straight line running obliquely from a point a little way in front of the siphonal inner openings, forward and upward to a point just below and slightly in front of the umbos of the shell. The anterior halves of the attachment of the two gills are separated by the visceral mass, but behind they are so joined that the excurrent chamber of the mantle cavity is completely separated from the incurrent one. Behind the visceral mass, the ascending lamellae of the medial demibranchs are attached to each other along their upper margins. The gill axes are here each suspended by a thin vertical septum, so that the excurrent chamber is divided into three compartments, two lateral and a medial, between the hind margin of the visceral mass and the lower end of the hind adductor muscle (Figure 2, ssg). Behind that point there is only a single tubular excurrent chamber, limited below by the horizontal septum of the mantle, laterally by the mantle proper, above by the lower surface of the kidney and the posterior adductor muscle, and behind the latter, an additional short horizontal septum of the mantle.

The outer demibranchs are not as wide as the inner, and do not extend as far forward. They are semilunar in shape, with short filaments at both ends, increasing gradually and regularly in length to the middle of the demibranch. The medial demibranchs extend a considerable distance forward, and actually begin well in front of the hind end of the attachment of the labial palps. The gills are eulamelibranchian, pleated, and all demibranchs have a groove along their free margin.

The labial palps are large, subtriangular, with convex anterior margin, concave posterior margins, and rounded ventral angle (Figure 1). They are attached along a straight line to the visceral mass by their dorsal margin. The two free sides of this triangle have a narrow strip lacking the numerous vertical ridges which cover the opposing surfaces of the labial palps. These ridges extend almost to the mouth; the medial parts of the palps are narrow, with simple free margins.

Only a few major features of the internal anatomy could be worked out. The two liver lobes, right and left, are rather small, and fill the periphery of the upper, anterior part of the visceral mass. The gonad, an ovary in the



one complete specimen available, fills the posterior half of the visceral mass peripherally, pushing dorsally over the stomach and under the pericardium. The antero-ventral part of the visceral mass has a large coiled mass of intestine (Figure 2).

The esophagus is short, opening into a large oval stomach. The interior of the stomach is much complicated with ridges and folds, details of which were not worked out. Most of the interior was covered by a loose lining of cuticular material, the gastric shield. A sorting area, of several oblique ridges on the left side, was not covered by the shield.

Each liver lobe consists of a thin-walled, branched tube. The liver follicles, glandular in appearance, are not branched, but clustered about the tips of the smallest branches of the hepatic ducts. Each follicle is about 0.1 mm in diameter.

Postero-ventrally, the stomach receives the style sac on the left, and the slightly smaller intestine opens beside it on the right. The style sac and intestine are completely separated, the former plunging down to the tip of the visceral mass and turning forward for a short distance, ending blindly. A well-formed crystalline style was present, after the clam had spent several days alive in the laboratory, and even after it had been opened for 2 days, maintained in the refrigerator at 4° C in sea water.

The intestine is thin-walled, light brown, and evidently without musculature. A dark brown fecal rope was passed along by ciliary activity. The intestine is unusually long, about several times the length of the shell. It is mostly coiled in the lower front part of the visceral mass, in a part of the hemocoel free from liver and gonad. Two parts of the intestine are recognizable on the basis of size, position and internal structure. The first part (duodenum) is imbedded in the ovary on the right of the style sac, and passes forward near the lower end of the visceral mass; it also forms the first few coils. It is about twice the diameter of the second part, the jejuno-ileal intestine. The latter makes up most of the coils, three of which loop symmetrically from side to side peripheral to the lower end of the liver; it then passes into the ovarian mass well ventrally, turns upward behind the style sac and enters the front end of the pericardium, beyond which point it may be called the rectum. After leaving the latter it passes between the two kidney lobes, over the outer surface of the posterior adductor muscle and opens into the hind part of the suprabranchial chamber of the mantle cavity, just in front of the excurrent siphon.

I could not determine the relative lengths of the large and small intestine, nor their junction. Perhaps it is a gradual transition. The large (duodenal) intestine has a huge lamella, or typhlosole, in it, much thicker than the

intestinal wall. At intervals of a few millimeters, this has short branches at right angles, but only along one side. These resemble buttresses. I could find no typhlosole in the small intestine, but perhaps one is present as a mere strip of cilia.

#### Feces:

The pseudofeces, consisting of particulate material assembled in the incurrent mantle cavity and rejected through the incurrent siphon, are poorly consolidated ropes of sediment, slightly larger than a millimeter in diameter and a few centimeters long.

True feces are of two types, which may be called ropes and pellets (Figure 4). The pellet type was seen in the

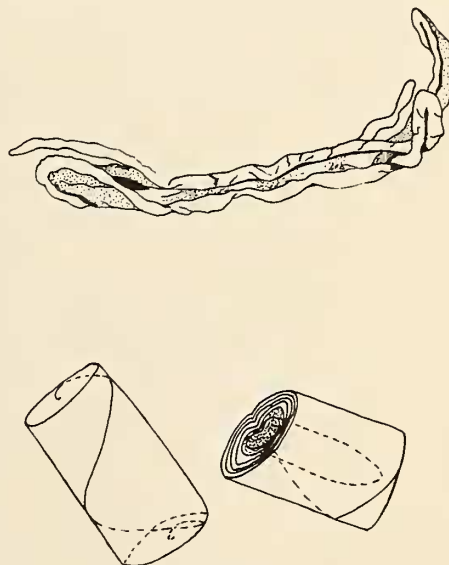


Figure 4

Feces. Rope type on right, an unopened pellet left above, and a pellet cut transversely on left, below.

rectum of the damaged specimens from the beach, and the rope type in the intestine of the intact specimen found in the bay. This specimen voided both types in the laboratory, and from that material Figure 4 was drawn.

The rope type of feces evidently passes through the intestine with little rearranging of the materials involved. It consists of a single strand, 80 to 100 mm long, with segments of dark tan material alternating with segments of dark olive color. The lengths of the two segment types are not constant. Probably the olive colored material is derived from the liver, and the tan material is of undigested particles which entered the mouth. These were not

studied in detail. The packaged configuration of the rope, bent back upon itself several times as shown in Figure 4, probably occurs as the rope is defecated into the supra-branchial mantle chamber. This package has been passed from the animal, as had numerous pellets.

The pellet feces were probably in the specimen when captured. They are constant in diameter, about 0.69 mm, and slightly variable in length, about 0.96 to 1.23 mm long, with longer pellets being more abundant. Each pellet is elaborately constructed. The pellets are smooth, regular cylinders with abruptly truncated ends, one being slightly convex, the other slightly concave. The surface is uniformly light tan colored, evidently of fine particles held compactly together with mucus. There is a single line, slightly incised, which begins in the middle of one end, makes about one complete turn on the lateral surface, and ends at the middle of the other end of the pellet.

Breaking a pellet open gently reveals a central cavity which seems not to extend quite to the ends. Its diameter is about  $\frac{1}{3}$  that of the pellet, and it is reniform in cross section. This cavity is loosely filled with granules of varying sizes, all larger than those of the outer part. The outer part of the pellet has about five layers, probably of only one continuous sheet, wrapped around the central cavity. The innermost layer is wider and less firmly consolidated than the others. The layers bend toward the concave side of the central cavity, and the spiral line on the outside seems to correspond to this also.

At higher magnification, the particles of the outer shell of the pellet all seem to be inorganic, angular granules, rarely as large as  $3\mu$ . No Brownian movement could be seen in a squash preparation in sea water, possibly because the mucous matrix was too viscous. The granules of the central cavity are irregular spheres, from 10 to  $14\mu$  in diameter. These are hyaline, golden brown and bright in reflected light. Also present were a few glassy angular flakes, colorless and polygonal, with sharp edges and angles. These are about 0.30 mm in maximum dimension. I was unable to find any organismal remains in the pellets, such as diatoms, even at  $970\times$  magnification.

The pericardium is a large, spacious, cuboidal sac located below the umbos (Figure 2). The ventricle of the heart surrounds the rectum, which transverses the pericardium lengthwise dorsally. The ventricle has two small projections antero-dorsally. The auricles are thin-walled triangular sacs diverted ventro-laterally. They nowhere touch each other. A light brown color on their exterior surface suggests a pericardial gland is present, but it does not extend onto the pericardial wall. There are two minute reno-pericardial openings on the post-ventral surface of the pericardial sac.

The kidney consists of two huge sacs, between the pericardium and the posterior adductor muscle. The posterior pedal retractor muscle passes between these sacs. Each sac is elongate, but bent upon itself, so that there is a dorsal moiety, beginning near the pericardium and passing backward to the adductor muscle, then turning forward ventrally to form the ventral moiety, which ends again at the pericardium. The large extensions of the kidneys into the mantle are projections from the upper moiety of each sac. The reno-pericardial passage is at the front end of the lower moiety of each sac, and a little farther back each lower moiety has a renopore opening into the excurrent mantle chamber, just in front of the post-pedal retractor muscle. The interiors of the kidney sacs are spacious; there are no trabeculae, but a smooth wall with large cilia, and numerous small holes opening into it (Figure 5). These are the ends of short narrow

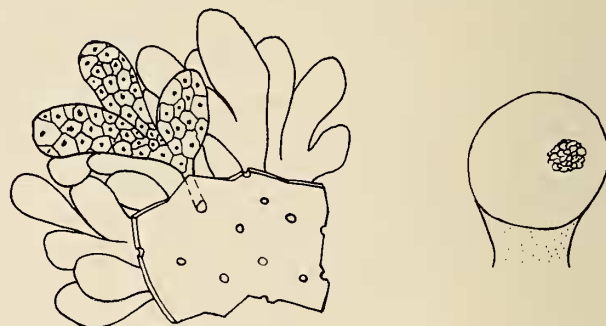


Figure 5

On the left, a part of the wall of the kidney, showing follicles extending from its outer surface and pores by which they open on the inside. Cells are shown in only one follicle. On the right, a single kidney cell from inside a kidney follicle.

ducts of the kidney follicles. Each follicle is branched two or three times; they are thin-walled, transparent sacs (about 0.3 mm diameter whose cavities are almost occluded by the bulbous ends of the excretory cells. These cells are part of the follicular wall, but they extend inward by narrow, short stalks. The free end of each cell is spherical, having a large vacuole which holds a light golden fluid. The fluid does not seem to mix with sea water. Each vacuole also has a spherical mass of golden brown, opaque granules.

The members of all three pairs of ganglia of the nervous system are fused, so that there are no commissures (Figure 2). The connectives between ganglionic pairs were not traced. The cerebral ganglia are just above the mouth. They are intermediate in size between the other



two pairs. The pedal ganglia are 0.19 mm long, and located at the front end of the base of the foot. The visceral ganglia are 0.3 mm long, and on the roof of the excurrent mantle chamber below the kidneys, but well in front of the posterior adductor muscle.

There are two prominent sense organs on the mantle, one on each side of the upper part of the inner end of the incurrent siphon, just in front of the median accessory mantle fold. These may be osphradia. Each is connected by a large nerve to the visceral ganglion on its side. They are elongate oval masses, about 0.1 mm wide and 0.3 mm long, and as high as they are wide.

The ovary of the intact specimen was a large, dendritically branched multifolliculate organ, the follicles being slightly less than 0.1 mm diameter, containing thousands

of eggs which appeared to be about ripe. The eggs are white, about  $44\mu$  diameter, with a large germinal vesicle  $27\mu$  diameter containing a nucleolus  $13\mu$  diameter.

There seems to be a single gonopore, opening into the front of the pericardial cavity just to the left of the rectum. If so, the eggs evidently must pass through the pericardium and kidney to reach the exterior.

#### Parasite:

A small cyst containing tapeworm larvae was attached to the outer surface of the intestine just below the stomach. It was white, and at first mistaken for a piece of the ovary. The cyst was thin-walled, elongate, with an irregular surface. It contained several dozen larvae, each coiled to form a sphere. Released from the cyst into sea water, the larvae squirmed with peristaltic movement and everted the terminal sucker. They attached with the lateral suckers (bothrydia) and moved along a glass surface by alternately attaching and releasing them.

The larva (Figure 6) is fusiform, about  $54\mu$  long. It is colorless, and the body is filled with small hyaline granules. The hind end tapers acutely, and the front end is rounded, with a deep, cup-shaped, muscular terminal sucker. This can be extended forward, or withdrawn to the level of the bothrydia. There are four elongate oval bothrydia, with small bases, attached symmetrically around the scolex. The cavity of each bothrydium is divided by two transverse partitions into three chambers (areolae) of equal size. No spines were seen at  $100\times$  magnification, nor could any internal anatomical details be made out.

#### Anatomical Discussion:

Most notable features of the anatomy of *Raeta plicatella* are the extension of the kidney into the mantle, the thin wall of the visceral mass, the atrophied foot, and the enormously long intestine. The abnormal ecological occurrence of the specimen on which most of this anatomical account is based might cast doubt upon some of the data on habits and anatomy. There is indeed an intrinsic conflict between the two: the long siphons and atrophied foot suggest this is a deep burrower which does not move about much in later life. An atrophied foot in late life of bivalves is probably more common than realized. Among species of the Galveston area I have seen such in *Periploma orbicularis* GUPPY, 1878 and *Diplothyra smithii* TRYON, 1862, neither closely related to each other nor to the Mactridae. But of the anatomical characters, I suspect only the small size of this specimen is abnormal in terms of other features; its presence above the substrate, as suggested by the epizoa growing on it, may indeed be unusual.



Figure 6

Tapeworm larva from cyst on intestine. Terminal sucker everted in complete specimen, retracted in the smaller figure.

The diversity in soft anatomy of the Mactridae appears to be larger than it is within most families of bivalves. I will not here try to summarize all of the literature on this subject, which, though extensive and scattered, constitutes a mere beginning in comparison to the number of species whose anatomies are unknown. A well-developed foot is present in all species previously studied, and the atrophied foot of *Raeta plicatella* is unique. Fusion of the mantle margin behind the pedal opening varies. In some species, the mantle lobes are completely free between the anterior adductor and the siphonal pocket. In others, the lobes are extensively held together along the posterior half of their margins by a fusion of a cuticular extension of the periostracum (*Lutraria*, *vide* YONGE, 1948). DALL (1898a) found free mantle lobes with papillae in *Resania*, but in *Zenatia* he says they are fused along their hind half, although he does not say whether the fusion is cuticular or represents cellular continuity. In *Raeta* the fusion is definitely cellular, and this genus therefore represents a third condition of the mantle margin.

A "fourth pallial opening" which is a small hole between the mantle edges just below the siphonal pocket, is present in some Mactridae and other families, according to KELLOGG (1915) and YONGE (1948), but such an opening is absent in *Raeta*.

The wall lamellae of the waste canal, as these structures were termed by KELLOGG (1915), have been given only passing attention in the literature except by that author and YONGE (1948), who termed them "mantle folds". DALL (1898a) described similar folds in the New Zealand genera *Resania* and *Zenatia*, but called them "sensory lamellae".

The siphonal lamellae and wall lamellae of the waste canal may be structures limited to the Mactridae, although YONGE says that folds similar to the wall lamellae, but probably differing in function, occur in the Tellinacean genera *Scrobicularia*, *Abra* and *Macoma*. A siphonal lamella forms a complete ring in the venerid *Saxidomus* as described and figured by KELLOGG, but whether this is homologous to the semicircular lamella of the incurrent siphon of the mactrids is unknown. Among mactrids, the siphonal lamella is said to be absent in *Lutraria* (YONGE, 1948), and both that and the wall lamellae are absent in *Spisula planulata* CONRAD, 1837, according to KELLOGG.

Whether or not gills are pleated or smooth, without vertical folds seems to be a character which varies at the generic or specific level. RIDWOOD (1903, pp. 237 ff.) found flat, homorhabdic (i. e., not-pleated) gills in four species of Mactridae on which he reported. Whether the pleated gills of *Raeta plicatella* have heterorhabdic fila-

ments at the grooves between the pleats was not determined.

The persistence of a crystalline style in bivalves which are not feeding, or at least while they are in the laboratory for some time with minimal food, is a phenomenon which seems to be characteristic of most marine ones I have studied. This contrast with the oysters and unionids, which seem to resorb the style quickly when not feeding, and reform it in the presence of food.

The opening of the gonad into the pericardium, so that the gametes transverse the kidney lumen and emerge through the renopore is a point which bears checking in further studies. PELSENEER (1911, p. 100) thinks such a condition is primitive, and limited to some protobranchs, Anomiidae and Pectinidae. From his reservations on the matter, it is evident that the gonopore is difficult to detect in bivalves.

Although MOORE (1931) called attention to the varied form of fecal pellets in marine mollusks, and suggested that careful study might yield valuable data on phylogeny and food habits, nothing further seems to have been published on the subject. MOORE did not describe the pellets of any mactrid bivalves. The feces of *Raeta plicatella* are markedly different from any he described in Pectinidae, Mytilidae, Tellinidae and Semelidae. The elaborate pellets of *R. plicatella* are very similar to those of the pholad *Cyrtopleura costata* LINNAEUS, 1758, but differ in minor details (unpublished data).

The presence of an osphradium in bivalves, homologous to that of snails, is a moot point. Only occasionally have such structures described above as an osphradium been noted. PELSENEER (1911, p. 112) calls these "sensory organ of the inhalent siphon", and cites them in the Mactridae.

The parasite found is evidently a larval tapeworm of the order Tetraphyllidea, the adults of which live in the intestine of elasmobranch fishes. Larvae of this type are called "*Scolex pleuronectes* MÜLLER, 1788" or "*Scolex polymorphus* RUDOLPHI, 1819", binomials which do not have exact taxonomic significance. As SHIPLEY (in SOUTHWELL, 1925, pp. ix - x) points out, "It is extremely difficult to identify the larval form of a cestode with its parents. It is a wise tapeworm that knows its own father". Apparently, the structures of the scolex in these larvae may vary considerably at different stages (ages) (SOUTHWELL, 1925, pp. 138 - 140). The one found in this study might be assigned to the family Phyllobothriidae, in lacking hooks on the scolex, yet the general form of the bothrydia is more like that of the other family in this order, Onchobothriidae, which, however, has no hooks in the scolex. Although most of these larval tetraphyllideans have been found in teleost fish, HYMAN (1951, p.



354) notes that they have been found in invertebrates of several groups, including mollusks, and she figures one (*l. c.*, figure 131 D) from the foot of a clam.

## Part II. SYSTEMATICS

### Review of *Raeta* and Related Genera:

#### *Anatina* SCHUMACHER, 1817

*Raeta* GRAY, 1853 has sometimes been considered a distinct genus, a position adopted here. Other writers have considered it indistinguishable from, or only a subgenus of, *Anatina* SCHUMACHER, 1817, or its junior synonym, *Labiosa* MÜLLER, 1832. The nomenclatural problem of *Anatina* versus *Labiosa* has been recently explored by KEEN (1961, q. v. for relevant bibliography), who gave good reasons for accepting the name *Anatina* as valid in the Mactridae. Moreover, she has shown that the type species of *Anatina* SCHUMACHER, 1817 is a western Atlantic species, *Mactra anatina* SPENGLER, 1802. This has been cited in much of the literature as *Anatina* or *Labiosa lineata* SAY, 1822, but is now correctly identified as *Anatina anatina* (SPENGLER, 1802).

Despite KEEN's study, the problem of whether to accept *Anatina* SCHUMACHER or *Labiosa* MÜLLER has not been put to rest. OLSSON (1961, p. 332) accepts *Labiosa*, as does VOKES (1967, p. 274), both apparently on the assumption that a use of the generic name *Anatina* by BOSC in 1816 is a validly proposed name, also a junior synonym of *Laternula* "BOLTEN" RÖDING, 1798. The latter is a relative of the anomalodesmacean genus *Periploma*. According to that line of reasoning, *Anatina* would therefore not be available to use in the Mactridae. The point of contention seems to revolve on what BOSC (1816, p. 492) said in defining *Anatina*; his description is here quoted:

"ANATINE, *Anatina*. Genre de coquilles bivalves établi par Lamarck aux dépens des Solens, sous la consideration d'une petite lame saillante à chaque valve en dedans où s'attache le ligament.

"Le Solen canard sert de type à ce genre, que est fort voisin des corbules et des Rupicoles. (B)".

If we consider, as KEEN has correctly done, the type cited by BOSC to be vernacular and therefore invalid, one might still argue that this is a genus validly described but without species. Whereas it may be entirely possible to conceive of a genus without species in the realm of pure thought, as may be done in modern logic, such a concept is absurd when applied to real biological entities.

*Anatina anatina* is a relatively rare shell on the beaches from New Jersey to Brazil. At Galveston it has not been found in the bays, but only as shells on the sandy beach and in a few dredged samples off shore. Apparently it does not occur in the Antilles.

The differences between the shell of *Anatina anatina* and the species from the West Coast of the Americas have been discussed by KEEN (1961), who pointed out that the West Coast species should be called *Anatina cyprinus* WOOD, 1828. I could find only a single valve of the latter species in the National Collection. It is from Topolobampo, Sinaloa, Mexico. OLSSON (1961) has given a description and further distribution records of this species under the name *Anatina anatina*. As far as I can determine, the two species from the coasts of the Americas are the only ones which should be put in the genus *Anatina* SCHUMACHER.

The synonymy of the genus *Anatina* and the two species included in it will not be repeated here, since KEEN (1961) has provided a meticulous account of these earlier in this journal, and I have nothing to add. The anatomies of the soft parts of these species is unknown, but it is worth pointing out that many recent authors (e. g., YONGE, 1948) refer to the anatomy of the "Anatinacea" when they are referring to the anatomy of the Anomalodesmacea of modern classification, i. e., the Periplomatidae, Lyonsiidae, Pandoridae and related groups. This confusion results from the fact that PELSENEER (1911 and earlier works), who paid scant attention to nomenclature, used the term Anatinacea based on *Anatina* as a genus in Periplomatidae. PELSENEER wrote most of what is known on the structure of the bizarre Anomalodesmacea, and most recent anatomists have unfortunately accepted his competency in nomenclature no less than in anatomy.

The shell of the type species of *Anatina* SCHUMACHER has been studied in more detail than has been previously reported, and a description of it will be useful for comparison with *Raeta* and related genera.

#### *Anatina anatina* (SPENGLER, 1802)

(Figures 7 to 10)

Shell very thin, fragile, white, translucent, elongate ovoid, the front end somewhat more sharply rounded than the hind. Size moderate (65 mm long, 43 mm high, 28 mm wide). Equivalve, and slightly inequilateral, the umbos being just behind the midpoint of the length. Umbos touching, minute and distinctly prosogyrous. The hind end of the shell gapes. The umbonal fourth of the shell has faint concentric corrugations, parallel with the growth striae, forming ridges and grooves on the inner surface.

The lower three fourths of the shell is smooth. A lunule is poorly defined by a shallow sulcus extending from the umbos in a broad arch about half the length of the

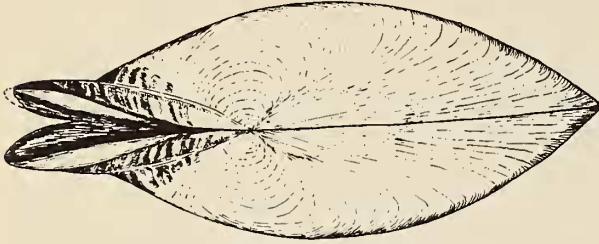


Figure 7

*Anatina anatina*, dorsal view. Galveston, Texas, length 43 mm.

antero-dorsal margin. This becomes wider toward its anterior end. On the medial side of the lunular sulcus is an opaque line not structurally differentiated on the outer surface. This is the line of attachment of the anterior hinge plate. The post-dorsal margin is about two-thirds as long as the antero-dorsal one. It is strongly turned laterally, enhancing the posterior gape of the shell. A low rib, scarcely higher than wide, extends from the umbo to the post-ventral part of the shell: this may be a corcelet lamella. In front of the rib, and separated from it by a space about half as wide as the space behind the rib, is a line defining an abrupt change in shell texture. This may be called the periostracal line. Along a narrow but poorly defined strip in front of the periostracal line vermiculate sculpture is evident. This is made up of minute wrinkles in the shell surface, joining and branching and mostly

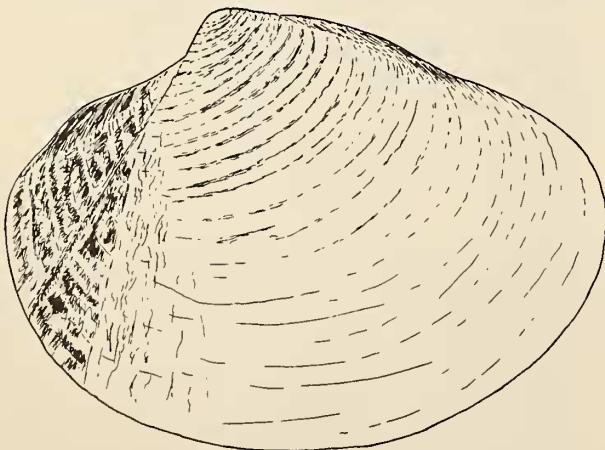


Figure 8

*Anatina anatina*. Galveston, Texas, length 33 mm

directed radially. They are not present over the smooth part of the disk in larger shells, but are uniformly distributed, although very faint, on all the adumbonal corrugated region. In fresh shells, the surface of the thin, persistent, faint tan periostracum is silky in reflected light. But behind the periostracal line, the periostracum is lusterless, and less persistent. There are only coarse growth lines in the shell behind the line, and a moderately thick layer of opaque chalky material is deposited there between the periostracum and ostracum.

The disk of the shell is distinctly swollen along a line from the umbo toward the antero-ventral angle. This gives the umbos the appearance of being directed backward, whereas in reality they are turned forward at their tips.

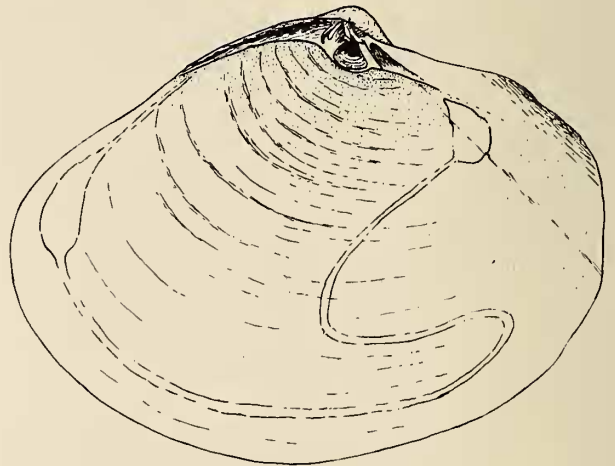


Figure 9

Interior of same valve as shown in Figure 8.

The pallial line is narrow, located close to the ventral edge of the valve, with slightly irregular dorsal margin. The anterior adductor scar is tear shaped, located directly on the pallial line; it has a pallial line extending dorsally from it to the front end of the hinge plate. Just above the anterior adductor scar the dorsal pallial line has a slight swelling, probably representing the anterior pedal retractor scar. The pallial sinus is large, rounded in front. It extends forward to a point below the umbos. Its lower side is well above the pallial line, not confluent with it. The posterior adductor scar is subtriangular, and the posterior pedal retractor scar constitutes a small constricted area confluent with the adductor at the dorsal tip of the latter. The corcelet ridge is evident internally as a shallow groove.



The hinge plate is slightly thicker than the valve. The front and hind halves extend along the front and hind dorsal margins for about half the length of the latter. The front half of the hinge plate is thus slightly longer than the other; this part of the hinge plate is strongly oblique to the valve surface, so that there is a deep space between the two. Its free margin is deeply excavated in a gentle curve, so that the trough between the hinge plate and valve is minimized. The hind half of the hinge plate is almost flat and horizontal, with its free margin almost straight. The resilifer is a triangular pit below the umbo, with its lower margin projecting as a rounded curve below the hinge plate.

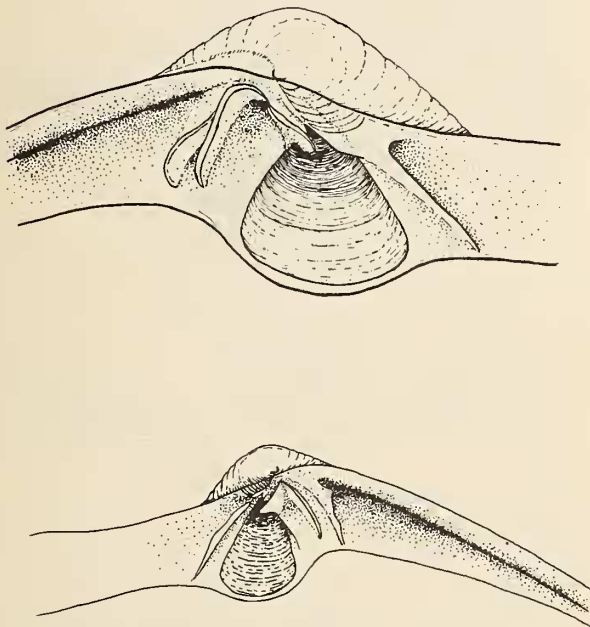


Figure 10

*Anatina anatina*. Hinge of shell. Upper is right valve. The valves are of different shells.

In the left valve, the cardinal tooth is moderately thick, and the sinus between the arms is large and deep. The sides of both arms are flat. The hind arm is about half as long as the front one. It projects over the resilifer as a free point. There is a thin antero-lateral lamella separating the front arm of the cardinal from the front hinge plate. A similar low, thin lamella is a little way behind the resilifer pit, separating it from the hind hinge plate. These two lamellae reach to the free margin of the plate, forming large oblique angles.

The attachment of the tensiliar ligament is a semi-lunar depression on the shell margin, beginning at and extending behind the umbo. This depression extends over the tip of the resilifer pit, concealing it. The front half of the curved (ventral) margin of the ligament pit is turned medially, and to its lower (front) surface is fused a small lamella projecting as a minute spine over the resilifer pit. This "spur" lamella is parallel to the hind ramus of the cardinal, separated from it by a deep groove which receives the hind cardinal ramus of the right valve.

In the right hinge the resilifer and ligamental shelf are much the same as in the left. There is also a single posterior lamella a little way behind the resilifer, separating it from the shallow trough of the hind hinge plate. The cardinal and antero-lateral lamellae are different from those of the left hinge. The cardinal is chevron shaped, with the posterior arm straight and about half as long as the anterior arm; the dorsal surface of the hind arm is fused to the medially turned edge of the ligamental plate, and the lower end of this arm extends free over the cavity of the resilifer; the medial (free) margins of the two arms have a deep excavation where they meet at the apex of the chevron. The anterior arm is sharply curved in its upper half, by being bent forward. This part is fused with the umbonal part of the antero-lateral lamella, which projects free from the lower part of the front arm of the cardinal, as a minute but thick and consistent structure.

The lateral lamellae of this species are probably homologous to the lateral teeth of other heterodonts, and indeed of other mactrids such as *Spisula* and *Mactra*. But in *Anatina* and *Raeta* they are more like cardinal teeth, radiating from the umbo, but not paralleling either the shell margin or the margin of the hinge plate; there is moreover only a single front and hind lateral lamella in both the right and left valves, whereas in *Mactra*, *Spisula* and some other genera, there is a single one before and behind in the left valve which fit between a pair at each place in the right valve. Also, in the latter genera, the laterals are parallel to the shell margin and, of course, to the margin of the hinge plate. The oblique, single lateral lamellae of *Anatina* and *Raeta* remind one of the laterals of the Cardiidae, which curve out as low ridges in a radiating arc from the umbo, on the inner surface of the shell.

Whatever the soft anatomy of *Anatina* may disclose, the characters of its shell seem sufficiently diverse from *Raeta* to separate the two generically; the presence of the periostracal line and the lateral flexing of the post-dorsal shell margin in *Anatina* are characters not present in *Raeta*. A lunule is defined in *Anatina*, but not in *Raeta*; the antero-ventral swelling of the disk is less pronounced

in *Anatina*; the corrugations are limited to the umbonal third of the shell in *Anatina*, but extend to the ventral margin in *Raeta*; the corcelet ridge is pronounced in *Anatina*, but its presence is indicated by a mere cessation of the corrugations near the post-dorsal margin, with no radial ridge *per se* in *Raeta*. In the right valve of *Raeta*, the anterior lamella is directly in line with the front ramus of the cardinal tooth, which is flat, and the ramus and lamella are separated by a notch (Figure 12). In *A. anatina*, the front ramus of the cardinal of the right hinge is bent above, almost as long as the front lamella, which is beside it and free from it below (Figure 10).

The vermiculate texture is common to both *Anatina* and *Raeta*. The periostracal chalk deposit, so pronounced in *Anatina*, may have become a lost character in *Raeta* s. s., but it is present in *Raetina*.

*Raeta* GRAY, 1853

The genus *Raeta* GRAY, 1853 (Ann. Mag. Nat. Hist., Ser. 2, vol. 11, p. 43) was briefly described and typed by original designation and monotypy, "*R. campechensis*", which is a junior synonym of *Lutraria plicatella* LAMARCK, 1818.

*Raeta plicatella* (LAMARCK, 1818)

(Figures 11 to 13)

- Lutraria plicatella* LAMARCK, 1818, Hist. Nat. Anim. sans Vert. 5: 470. Not figured; refers to GMELIN p. 3257, and CHEMINIZ Conch. Cab. 6, tab. 23, fig. 231 with a question mark. Type locality, "Probablement l'Océan indien."
- Lutraria canaliculata* SAY, 1822, Journ. Acad. Nat. Sci. Phila. 2: 311 - 312. Not figured. Type locality, "Maryland and as far south as East Florida."
- Mactra campechensis* GRAY, 1825, Ann. of Philos., N. S., 9: 135. Not described or figured; refers to "List. 304 (sic) f. 141", evidently LISTER, 1770, the second or Huddlesford edition, where f. 141 of plate 308 (not 304) is a creditable figure of this species, with the words, "a sinu campeche" evidently indicating the type locality as the Bay of Campeche, Mexico.
- Raeta perspicua* HUTTON, 1873, Cat. Marine Moll. New Zealand, p. 65. Not figured. Type locality (erroneously) New Zealand. 1913, SUTER, Man. New Zealand Moll., p. 970, Atlas (1915), pl. 60, fig. 5. OLIVER (1923: 184) notes that this is a synonym of *R. canaliculata* SAY, incorrectly attributed to New Zealand.
- Labiosa (Raeta) plicatella* LAMARCK. 1917, LAMY, Journ. de Conchyliol. Ser. 4, 12: 353 - 354; pl. 7, fig. 6 (photograph of holotype). 63

The description and figures cited by LAMARCK in describing *Lutraria plicatella* were insufficient to recognize this species, and he furthermore thought it came from the

Indo-Pacific area, but expressed doubt. LAMY (1917) published a photograph of the holotype of LAMARCK's species which is unmistakably the species of the western Atlantic coasts. Meanwhile, it has been extensively cited in the literature under the trivial name applied by SAY, and in combination with various generic names. HUTTON redescribed and named this species from a shell which he attributed to New Zealand, but which had evidently come from elsewhere, as pointed out by OLIVER. There are apparently no living species of *Raeta* or *Raetella* in New Zealand.

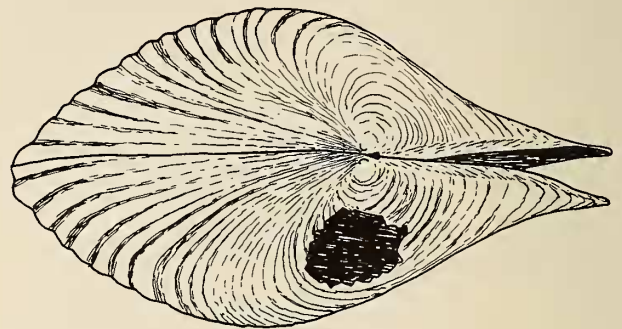


Figure 11

*Raeta plicatella*, dorsal view of shell 25 mm long, Galveston Beach. The hole was probably made by a shore bird.

Shell of moderate size (length 72, height 60, width 40 mm), thin, white, ovoid in side view, equivalve and gaping slightly behind; subequilateral, the umbos being slightly closer to the hind end. Umbos small, but swollen and prominent, touching each other and turned slightly but distinctly forward. The whole outer surface has prominent concentric ribs, rounded, poorly defined and with the grooves between slightly wider. These extend through the shell structure, producing a corrugated inner surface. In shells longer than 55 mm, the ribs tend to be more irregular and obliterated along the margin, with the inner surface smooth there. Fine radial wrinkles, closely spaced, are present on the ribs. These are most prominent on the lower third and hind slope of larger shells, where they extend into the grooves as well, and tend to anastomose. The wrinkles are part of the outer shell layer. The thin, light tan periostracum is smooth, closely adherent, but absent from even slightly worn shells. The front dorsal margin is gently convex, and continues in an even curve into the ventral margin, which is more convex. The hind dorsal margin has about the same curvature as the front, but it is shorter, slopes more abruptly from the hori-



zontal; it meets the ventral margin in an obtusely rounded angle. There is no lunule; a narrow corcelet is poorly defined along the post-dorsal margin, extending to its post-ventral angle. This is formed merely by the concentric ribs turning abruptly umbonad along this line, becoming much weaker, and lacking the vermiculate micro ridges present in front of the line.

The disk is greatly inflated from the umbo to the antero-ventral angle. A wide, shallow trough separates the disk from the post-dorsal slope, which is somewhat flattened.

The shell margin inside is smooth and sharp, the surface of the interior is subporcellaneous. The pallial line is thin, but prominent and continuous, with a large sinus reaching half-way forward and with rounded or usually acutely pointed tip. Its upper border has a rounded angle midway its length. The lower border is well separated from the pallial line proper. The anterior adductor muscle scar is thin and very elongate, narrowing acutely above.

The hind one is oval to subquadrate, with a small posterior pedal retractor scar confluent at its upper end.

The hinge plate is only slightly thicker than the rest of the shell. The hind half is vertical and flat, and of uniform width. It extends along the upper two-thirds of the hind margin. The front part has the shape of an acutely tapered triangle; it is about a third as long as the hind part. It is attached obliquely to the shell. Directly below the umbo there is a large triangular resilifer, deeply excavated and extending to the tip of the umbo, but its upper third is covered by shell. The base of the triangle is well below the rest of the hinge plate margin. The ligament is entirely internal, and divided into resilium and tensilium, well separated. The resilium has the form of two tapering horns, slightly curved, with their apices in the covered upper parts of the resilifers, directly below the umbos, and the faces of their circular bases meeting in the midline. The faces of the opposed bases are concave, with only the peripheral margins touching. The concavity extends upward on the medial side of the horns to the tip of each. The outer, lateral side of each horn is flattened and about a third again as large as the opposing faces, so that the two halves of the resilium have the shape of an hour glass when viewed along the median plane of the animal.

The tensiliar part of the ligament is elongate lanceolate, short, attached at the shell margin beginning just below the umbos, and with its axis sloping ventrally, away from the shell margin behind. Only the anterior tip is visible externally. The tensilium is attached to a hinge buttress, a lamella which parallels the hind side of the resilifer triangle, and which extends almost to the free hinge margin. It is obliquely attached to the hinge plate, so that its medial surface, to which the tensilium is attached, slopes downward and backward toward the resilifer cavity. Its upper third is attached to the shell margin completely roofing over the subumbonal tip of the trough on the hind half of the hinge plate. The lower half of the tensiliar lamella is acute, and extends over the trough slightly.

Along the tensiliar lamella, below the tensilium, there arises an oblique buttress lamella, of the hind ramus of the cardinal tooth. It completely conceals the upper fourth of the resilifer cavity, covering the apical end of the resilium. Along the margin of this lamella which approaches the cardinal tooth, there is a sharp spine projecting toward the middle of the base of the resilifer.

A single cardinal tooth in each valve has the shape of an inverted V, with the rami diverging at slightly less than a right angle, and the apex directly below the umbo, separated from it only by the thin hinge margin. The left cardinal fits into the cavity of the right one. The outer

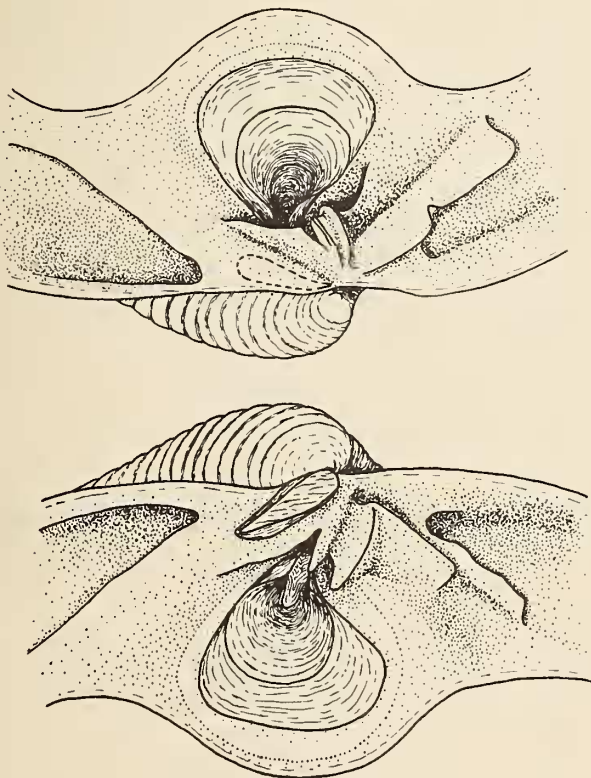


Figure 12

Right (upper) and left hinges of *Raeta plicatella*. The tensiliar ligament is present in the left valve only, but the two halves of the resilium are present in their respective valves.

faces of the left cardinal are smooth and flat, but the two rami are thick and fused so that the cavity of its chevron is nearly filled solid, leaving only a vague medial sulcus on the ventral side. Each cardinal tooth is about half as high as the width of the hinge margin, and the hind ramus of each projects over the resilifer.

A deep groove along and above the base of each ramus of the left cardinal receives the right cardinal. This groove



Figure 13

Upper: *Raeta plicatella* from Galveston, 63 mm long.

Lower: *Raeta undulata* from Topolobampo, Mexico, 71 mm long.

is formed behind by the margin of the subteniliar buttress and its prominent spine, and in front by a lamella of moderate thickness, normal to the hinge plate and parallel to the anterior ramus of the left cardinal. This is the anterior lateral lamella. Its umbonal half is low, and connected to the inner side of the shell by a small buttress parallel to the hinge plate; this is the anterior buttress of the cardinal tooth and it roofs the extreme tip of the anterior hinge plate trough. The lower half of the anterior lamella is raised into a quadrate tooth-like process.

In the right valve the hind ramus of the cardinal tooth is fused with the spine of the buttress arising below the tensilium, but not completely, so that it and the spine appear as a bifid tooth. The front ramus is the same length as the hind one, but it appears to be twice as long, because of a quadrate lamella directly below and in line with it. It is separated from the quadrate lamella by a small but consistent notch. This quadrate lamella is the antero-lateral lamella. The front ramus of the right cardinal has a thick lamellar buttress extending from its free margin outward and upward to the inner surface of the shell, and roofing the trough of the hinge plate.

In both valves there is a single posterior lateral lamella, running from the umbo toward the ventral margin. This lamella is bent upward toward the shell margin, so that its attachment on the hinge plate is oblique, and poorly defined in medial view. Evidently these two lamellae are directly opposite each other in the closed shell, and one does not insert above the other, since neither crosses the median plane. But they may be homologous to the posterior lateral teeth of other mactrids.

*Raeta (Raeta) undulata* (GOULD, 1851)

(Figure 13, lower shell)

*Lutraria undulata* GOULD, 1851, Proc. Boston Soc. Nat. Hist. 4: 89. Not figured. Type locality: La Paz, Lower California. 1853, GOULD, Boston Journ. Nat. Hist. 6: 391; plt. 15, fig. 7.

OLDROYD (1924) has copied the English translation of the description by GOULD of this species which he published in 1853. She also republished (*l. c.*, plt. 21, fig. 11) his original figure, an external view of a left valve. His figure 7 also includes a dorsal view of both valves, showing a prominent posterior gape. The figure he published shows very regular corrugations from beak to ventral margin, but in the larger specimens I have seen, these ridges tend to be obliterated toward the lower margin, more so than in *Raeta plicatella*. Perhaps his figure was drawn from a juvenile shell.



The shell of *Raeta undulata* is similar to that of *R. plicatella* in the coarse corrugations well covered by vermiculations, and in the hinge, which also has an oblique postero-lateral lamella in each valve. It differs chiefly in the more rounded, posterior end of the shell, in having the umbos about midway the length or slightly forward of that point, instead of well behind, and the corcelet line along the postero-dorsal shell margin is distinctly farther from the margin than in the east coast species. The chalk deposit of the periostracum seems to be absent. More extensive synonymies are given by OLSSON (1961), all to secondary references however. This species may have the same ecological distribution as the one on the East Coast, just beyond the surf zone along sandy shores. KEEN (1958) notes that "Beach valves are fairly common, but entire specimens are hard to find, even by dredging".

(*Raetina*) DALL, 1898

*Raetina* DALL, 1895, Proc. Malacol. Soc. London 1: 212, Type *R. indica* DALL (nom. nud.).

*Raetina* DALL, 1898, Trans. Wagner Free Inst. Sci. 3 (4): 822, Type by O. D. and M *Raeta* (*Raetina*) *indica* DALL, 1898, which is a junior synonym of *Mactra pellicula* REEVE.

This is similar in size and shape to *Raeta* s. s. The hinge plate is thick, almost vertical behind, and the groove on it is shallow and rounded in cross section. Sculpture is continuous top to bottom, and from front to hind end; it consists of corrugations evident on the inner surface of the shell, and the corrugations are in line with the growth lines, not oblique. Vermiculate texture is present, but very weak and limited in area.

The main reasons for recognizing this as a distinct subgenus are two: (1) the sculpture is more delicate, the corrugations being finer and more closely spaced than in the typical subgenus; (2) the posterior lamella, running obliquely from the umbo across the front end of the hind hinge plate, is absent in this subgenus. Chalky deposits in this periostracum, which occur in *Anatina*, may be present in *Raetina*, but seem to be absent in *Raeta* s. s.

This genus was essentially a nude name as of 1895, diagnosed only by indication of the type species, which was not described until 1898.

*Raeta* (*Raetina*) *pellicula* (REEVE, 1854)

(Figures 14 and 15)

*Mactra pellicula* "DESHAYES" REEVE, 1854 (May). Conch. Icon 8: Monograph *Mactra*, plt. 21, fig. 124. Type locality: Japan.

*Mactra anatinoides* REEVE, 1854. Conch. Icon. 8: Monograph *Mactra*, plt. 21, fig. 123. Type locality unknown.

*Mactra pellicula* DESHAYES, 1855. Proc. Zool. Soc. London 22: 68. Not figured. Type locality: "Japan (col. Cuming)."

*Raeta grayi* H. ADAMS, 1872. Proc. Zool. Soc. London, p. 13, plt. 3, fig. 23. Type locality: Borneo.

*Raeta abercrombiei* MELVILL, 1893. (In MELVILL & ABERCROMBIE, 1893) Manchester Lit. & Philos. Soc. Mem. & Proc. Ser. 4, 7: 32 (nom. nud.); MELVILL, 1893, Ibid., p. 65; plt. 1, fig. 25. Type locality: Bombay, India.

*Raeta* (*Raetina*) *indica* DALL, 1895. Proc. Malacol. Soc. London 1: 212 (nom. nud.).

*Raeta* (*Raetina*) *indica* DALL, 1898. Trans. Wagner Free Inst. Sci. 3 (4): 882-883, footnote. Not figured. Type locality: Bombay, India.

*Anatina* (*Raetina*) *indica* DALL, 1925. Proc. U. S. Nat. Mus. 66 (17): 2; plt. 20, fig. 2. Holotype.

*Raeta jickelii* STURANY, 1905. Nachrichtsb. d. deutsch. Malakol. Ges. 37<sup>th</sup> year, pp. 133-134; text figs. a, b, and c, p. 133. Type locality: "Massaua" (Massawa, Ethiopia, southwest coast of the Red Sea).

*Raeta magnifica* YOKOYAMA, 1922. Journ. Coll. Sci. Tokyo, 44: 132; plt. 8, figs. 12, 13. Type locality: Fossil, Tega (Kizaki), Japan.

*Raeta fragilis* GRABAU & KING, 1928. Shells of Peitaiho, pp. 190-192; plt. 7, fig. 54. Type locality: Peitaiho (Yellow Sea, China).

This species has a very wide range, from the shores of the Red Sea, to India, Borneo, China and Japan. It evidently shows some variation in form, particularly in the

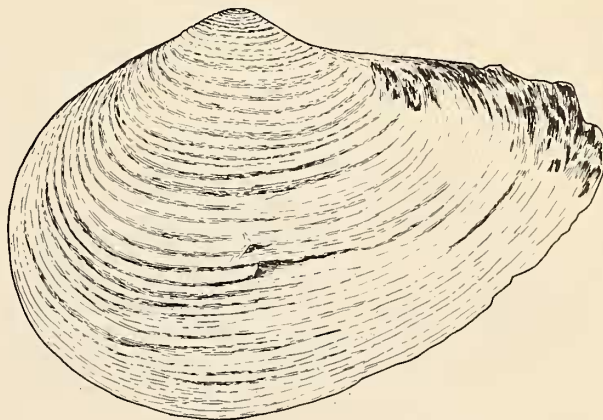


Figure 14

Holotype of *Raeta* (*Raetina*) *indica* DALL (= *Raeta pellicula*). The dark shading along the postero-dorsal margin indicates periostracal chalk deposit. Length, 43 mm.

length and acuteness of the rostrum. The short-rostrate forms are what authors have called *Raeta anatinoides* (REEVE) and, judging from the figure, *R. grayi* H. ADAMS. TOMLIN (1924) pointed out that the species names pub-

lished by REEVE (1854) in his monograph of *Mactra* predate all species named by DESHAYES in 1854 and 1855, even though REEVE attributes many names to DESHAYES. For exact date on the several species, see the paper by TOMLIN. Elsewhere TOMLIN (1931) declares *R. abercrombiei* identical with *R. grayi* after comparing the holotypes of the two species. Although DALL was quite sure his *R. indica* was distinct from *R. abercrombiei*, the only differences he cited were "form and proportion". The holotype of *R. indica* DALL shows no significant differences from a shell in the National Collection from Japan, which in turn fits quite well with the concept of *R. pellicula* REEVE. No one who has studied the group seems to have seen more than a few shells from different places, and the above synonymy can only be tentative.

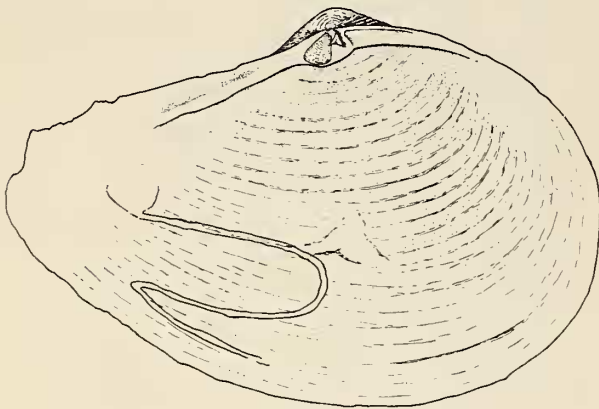


Figure 15  
Interior of same valve as shown in Figure 14.

Like the species of *Raeta* s. s., all records of this species are from the beaches of continents or the larger continental islands. It may be absent in the small oceanic islands of the Indo-Pacific, which seem indeed to have few mactrids of any genus. Probably this species lives at the outer edge of the surf zone on sandy shores.

The following description is based on the holotype of *Raeta indica* DALL, which is a single left valve, USNM 90276, with the words "Bombay" and "Wesleyan Univ." on the label.

Length 43, height 28, semidiameter 9 mm. Shell elongate ovoid, front end evenly rounded, hind end drawn out in an obtusely rounded rostrum. Probably equivalve, and almost equilateral, the umbos being slightly closer to the front end. Umbos prominent, touching, turned slightly forward. Shell very thin, translucent, with numer-

ous concentric ribs and troughs, which are undulations of the shell substance affecting both surfaces. The undulations are regular, from umbo to ventral margin, and continuous, except along the post-dorsal slope. They are parallel to the growth striae. Color white. No lunule. Corcelet (or escutcheon?) defined only by rapid diminution of the ribs along a poorly defined line near and parallel to the post-dorsal margin. No epidermis is evident, but there is a chalky white deposit postero-ventrally. A few faint vermiculations, similar to those of *Raeta plicatella*, are evident only along the post-ventral part of the valve.

The roundly pointed pallial sinus reaches as far forward as the umbo. Its lower margin is separated from the pallial line. Muscle scars could not be seen in the slightly worn holotype (but DALL illustrated them as typical of *Raeta* s. s.). The hinge is typical of *Raeta*, except that there is no hind radiating lamella between the resilifer and the groove of the post hinge plate. The comparable buttress of the front hinge plate groove is slightly broken, but it has a thick base. The posterior gape between the valves must have been small.

I cannot see any specific differences in the holotype and a pair of matched valves from Japan (Hirase Coll., US NM 344967, 53 mm long, 41 mm high). The Japanese specimen is larger, not as acuminate rostrate behind. There is no chalk deposit on its posterior slope, but a faint, narrow corcelet ridge seems to be present, slightly forward of the line medial of which the concentric ribs become mere growth striae, though pronounced.

The form of both the Indian and Japanese shells is easily distinguishable from *Raeta plicatella* and *R. undulata*, the ribs are more numerous and finer, the posterior lateral lamella is lacking in both specimens of the oriental species.

#### *Raetella* DALL, 1898

*Raetella* DALL, 1895. Proc. Malacol. Soc. London 1: 212. Type by O. D. and M. *Raetella tenuis* (HINDS MS.) DALL (nom. nud.).

*Raetella* DALL, 1898. Trans. Wagner Free Inst. Sci. 6 (4): 882 - 883. Type species by O. D. *Raetella tenuis* "HINDS" DALL, 1898, which is a junior synonym of *Poromya pulchella* A. ADAMS & REEVE, 1850.

*Raetellops* HABE, 1952. Genera of Japanese Shells, Pelecypoda No. 3: 197, as subgenus of *Raeta* GRAY, 1853. Type by O. D., *Poromya pulchella* A. ADAMS & REEVE, 1850.

This name was essentially nude when proposed by DALL in 1895, being diagnosed only by designation of the type species, which was not described until 1898.



Shells of this genus are much smaller in size than those of *Raeta*, and the ribs of *Raetella* are proportionately coarser. They are, moreover, slightly oblique to the lines of growth. The shells have a peculiar opalescent luster, which DALL called a "pseudo-nacreous surface". Vermiculate texture and chalky periostracal deposit are absent. Although DALL (1898, p. 882) said the "dorsal areas [are] well defined", there is no structural feature on the external surface defining them; their presence is merely simulated by the attachment of the hinge plate showing through the translucent shell. The hinge plate lamellae are very thin, and the front one is only slightly shorter than the hind one. Both front and hind parts are almost horizontal, with the space between them and the adjacent valve surface very deep. In *Raeta* and *Raetina* the posterior half of the hinge plate is essentially vertical and thick, with swollen, rounded free margin. The lateral teeth are parallel to the hinge plate margin, not strongly oblique to it, as in *Raeta* and *Raetina*. Moreover, there is a single hind lateral in the left valve, but two in the right, in the pattern quite general in Mactridae. But there is only a single, short antero-lateral in each valve. This genus may extend to greater depths than do *Raeta* or *Raetina*, which, like most mactrids, are shallow water inhabitants. As presently known, it seems limited to the eastern coast of Asia and larger continental islands along it.

*Raetella pulchella* (A. ADAMS & REEVE, 1850)

(Figures 16 to 19)

*Poromya pulchella* A. ADAMS & REEVE, 1850. Voy. Samarang. Zool., Mollusca, p. 83; pl. 23, fig. 1. Type locality: Shores of Borneo.

*Mactra rostralis* "DESHAYES" REEVE, 1854. Conch. Icon. 8, Monogr. *Mactra*, pl. 21, fig. 119. Type locality: "China Seas?"

*Mactra rostralis* DESHAYES, 1855. Proc. Zool. Soc. London, p. 69. Not figured. Type locality: Japan.

*Raeta yokohamensis* PILSBRY, 1895. Cat. Marine Moll. Japan ... collected by F. Stearns, p. 119; pl. 3, figs. 4, 5. Type locality: Yokohama, Japan.

*Raetella tenuis* "HINDS" DALL, 1898. Trans. Wagner Free Inst. Sci. 3 (4): 883 (footnote). Not figured. Type locality: Hong Kong Harbor, about 8 feet of water.

*Raeta elliptica* YOKOYAMA, 1922. Journ. Coll. Sci. Tokyo 44: 131-132; pl. 8, fig. 7. Type locality: Fossil, Tega, Kamenari, Kioroshi (Japan).

*Raetella rostralis* has been considered a synonym of *R. pulchella* by most authors, as pointed out by LAMY (1917). On the basis of the original descriptions and illustrations of the several nominal species, I agree with HABE (1952) that *Raeta yokohamensis* and *Raeta elliptica* should be added to the synonymy. The specimen on which DALL

based his name *Raetella tenuis* "HINDS" also seems con-specific. HINDS seems never to have named such a species, and DALL (1898) received the name from P. P. Carpenter, who evidently took it from a label in the British Museum.

The following description is based on the holotype of *Raetella tenuis* "HINDS" DALL. The type lot is USNM 519, and the label has written on it "4-8 ft., mud, in harbor, Hong Kong, Stimpson". The holotype consists of disjoined valves of one shell; the right valve is only broken around the ventral and posterior margin, but the left is fragmented into several large pieces.

Shell small (13 mm long, 10 mm high, 3.0 mm semi-diameter), ovate in profile, evenly rounded in front and

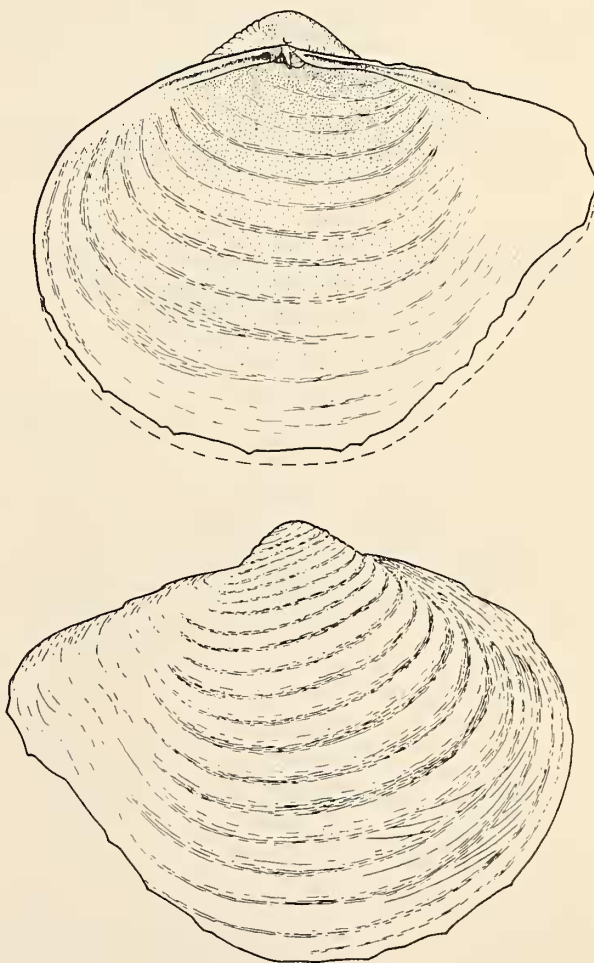


Figure 16

Holotype of *Raetella tenuis* "HINDS" DALL (= *Raetella pulchella*).  
Length, 13 mm.

below, drawn out in a short but rather acute rostrum behind. The disk is very inflated, almost hemispherical, but the inflation is even, without a prominent axis from umbo to antero-ventral margin. Umbo  $5/7$  the length from the front end.

Color white. A thin, closely adhering periostracum is light tan. The outer surface has a faint opalescent iridescence. Sculpture of about 23 concentric ribs, which are regularly spaced from umbo to ventral margin, but which do not extend to the antero-dorsal margin nor onto the rostrum. There is a slight, very broad, shallow sulcus between the disk and the post-dorsal region, but no demarcation of an escutcheon or corcelet. There is no chalky deposit in the periostracum, and no radiating vermiculate texture. The concentric ribs are slightly oblique to the lines of growth, and this is most prominent on the antero-ventral part of the disk. A lunule is simulated by the attachment of the anterior hinge plate.

Shell very thin, the ribs forming undulations on the inside, which is porcellaneous. Attachment scars not evident in the holotype.

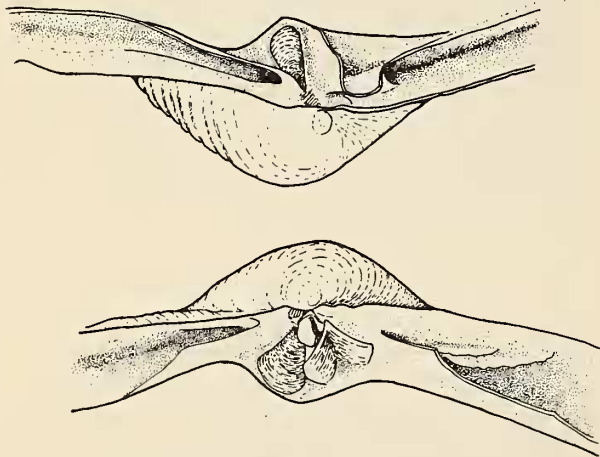


Figure 17

Hinge of holotype of *Raetella tenuis* "HINDS" DALL  
(= *Raetella pulchella*)

In the right valve a V-shaped cardinal tooth is adjacent to and points toward the umbo. The two arms are about equal in length, moderately thick, and with a broad, deep space between them. A deep cleft separates the medial part of their junction, at the apex of the V (poorly shown in Figure 17; see Figure 19). The posterior arm is separated by a narrow space from the front edge of the resilifer. Along the base of the anterior ramus there is a very thin buttress which crosses obliquely the space

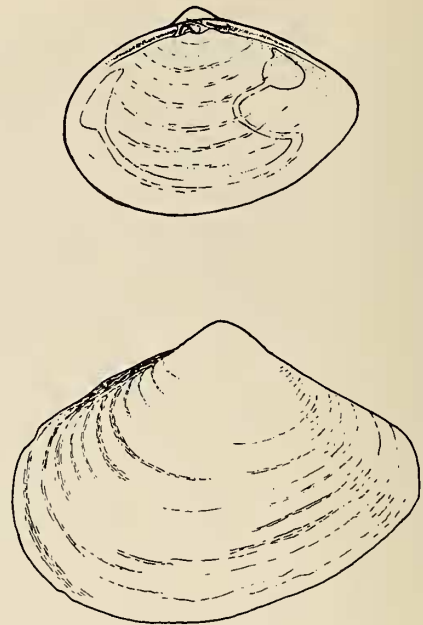


Figure 18

Upper: *Raetella pulchella* from Japan (USNM 249247) showing pallial sinus. Lower: *Raetella pulchella* from Fukura, Awaji, Japan (USNM 344966) 23 mm long. Note relatively smooth surface and poorly rostrate hind end.

over the cavity of the anterior hinge plate and attaches to the shell. A lamella in line with the anterior arm of the cardinal and also the anterior hinge plate lamella seems to be broken off, flush with the latter, in the right valve of the holotype (see Figure 19). The anterior hinge plate is very thin, with sharp free margin. It is almost horizontal, paralleling the dorsal margin of the shell and attaching rather far laterally. The cavity between the front hinge plate and the shell is thus very deep and narrow. The front hinge plate lamella is only slightly shorter than the hind one. The hind hinge plate is not so wide as the front, and the cavity between it and the shell is not so deep. No escutcheon area is defined on the outer surface by its attachment. It is equally thin, with sharp margin. Along the umbonal fourth this plate is extended medially slightly, forming a lateral tooth. Above it on the margin of the shell is another very slight lamella, not as long as the lower one, forming an upper posterior lateral tooth. The resilifer is small, triangular, directed downward from the umbo. Tensilium very short, directly under the umbo, and not separated from the resilifer by any shelly material except the small ledge on which it sits.



Hinge of the left valve similar to that of the right. The two rami of the V-shaped cardinal tooth are thicker, smaller, and evidently fit inside the right cardinal. Above the left cardinal and between it and the umbo is a small but prominent tooth-like process, with an inverted V-shape, the front ramus of which is very short. The hind ramus of this little tooth margins the upper part of the resilifer. A lamellar extension of the anterior hinge plate seems to be present at the umbonal end but it is badly broken. There is no dorsal lateral tooth on the shell margin. A very thin prominent lamella radiates from the umbo and separates the hind hinge plate from the cardinal area. Two small lamellae in the front hinge plate cavity of the left valve do not extend to the median plate of the shell, and are possibly abnormal.

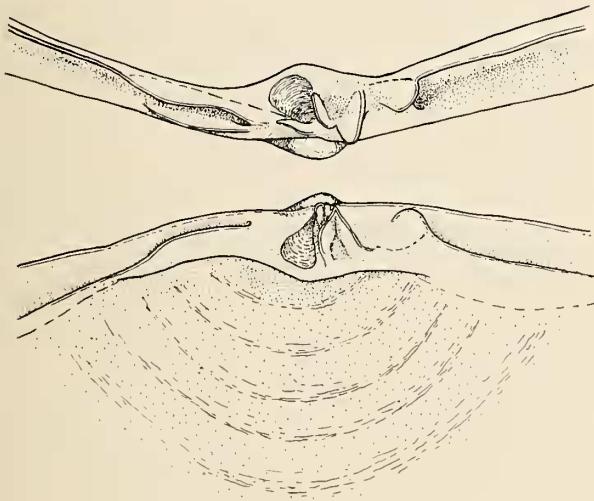


Figure 19

Hinge of *Raetella pulchella* from Japan (USNM 249247). The drawings were made at slightly different angles, causing the resilifer of the left (lower) valve to appear smaller than that of right hinge.

The holotype of DALL's nominal species is more inflated over the disk and more rostrate behind than most specimens of the 14 lots in the National Collection from Japan. It fits the concept of "*Mactra*" *rostralis* better than "*M.*" *pulchella*, but I think it is only an extreme variant of this highly variable species (cf. Figure 18). Some shells from Japan are larger (20 mm long, 14 mm high). The Japanese shells are slightly gaping behind, and equivalve. Sculpture on them varies considerably, some shells being almost smooth, with ribs limited to the ventral part, not present on the umbo. Most Japanese shells are less rostrate

behind than is the holotype of DALL's species; they are more equilateral, and not as inflated over the disk.

Figure 19 is a drawing of the hinge of a Japanese specimen, showing the prominent short anterior lateral tooth, directly on the hinge plate margin. Each tooth curves outward from the umbo, as shown by the dotted lines at their bases. The left antero-lateral slips above the right one when the valves close. The left valve has a single postero-lateral tooth, which fits between the two on the right valve. All these postero-laterals are developed as elongate lamellae directly on the valve margin and hinge plate margin, and parallel to them.

A large lot from Siam (USNM 477293) has very thin shells which are non-rostrate, well sculptured, and of a uniform small size.

### SPECIES INCERTAE SEDIS

#### *Raeta meridionalis* TATE, 1889

(Figure 20)

*Raeta meridionalis* TATE, 1889. Trans. Proc. Roy. Soc. South Austral. 11: 61; pl. 11, fig. 3. Type locality: Aldinga Bay (South Australia).

?*Labiosa meridionalis* TATE, 1889. HEDLEY, 1900. Proc. Linn. Soc. New South Wales 25: 497; pl. 25, figs. 5-9. Locality: Chinaman's Beach, Middle Harbour (Australia).

TATE's original description of this species is here quoted, and Figure 20 (left) is a tracing of his original drawing.

"Shell whitish, very thin, translucent; ovately-suboblong, moderately convex antemedially, posteriorly gaping; umbo subacute, curved forward, situated in the anterior three-sevenths. "Anterior margin regularly rounded, ventral margin strongly arched; dorsal line sloping on both sides, more so in front than behind; posterior side narrowed and depressed, its margin somewhat squarely truncated and slightly reflected. There is an ill defined depressed post-dorsal area, but no umbonal ridge.

"Sinus widely rounded, horizontal, reaching to the center, visible on the exterior.

"Surface marked by fine lines of growth, which become more conspicuous and finely wrinkled on the post-dorsal area.

"Dimensions: Antero-posterior diameter, 35; umbo-ventral diameter, 30; sectional diameter of left valve, 8 millimeters.

"Locality - one valve collected by Mr. Magarey on the beach of Aldinga Bay."

The species described by TATE has the shape of *Mactra anatinoides* REEVE, which I have considered a junior synonym of *Raeta pellicula*. But the sculpture is most unusual for a *Raeta*. It is apparently so thin that the pallial sinus shows through the shell, yet strong concentric corrugations seem to be lacking, and there is no corcelet line or ridge along the post-dorsal slope. I have seen no specimens. This species evidently lives near the shore of sandy

beaches and it may be quite rare. A copy of the original figure is given by COTTON & GODFREY (1938) and by ALLEN (1959). Incidentally, COTTON's (1961, p. 343) reference to the original description of this species ("TATE, 1887, Trans. and Proc. Roy. Soc. So. Austr. 9: 68 - 69, pl. 5, fig. 4, *Montacuta meridionalis*") is evidently in error, for the description and figure of *Montacuta meridionalis* TATE, 1887 clearly refers to a leptonid bivalve, and not to *R. meridionalis* (TATE, 1889).

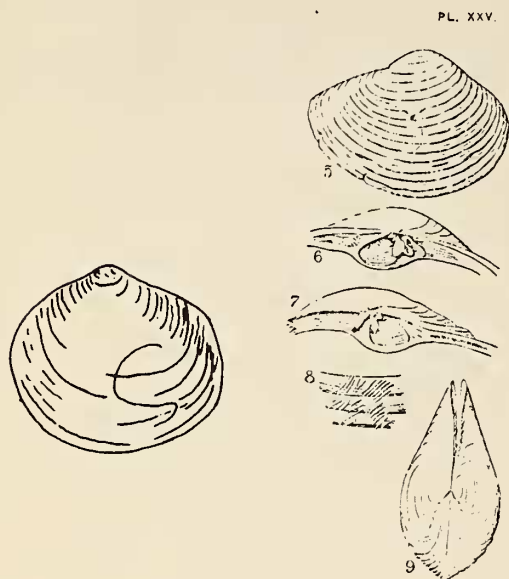


Figure 20

Left: Tracing of figure 3 of plate 11, TATE, 1889, the original drawing of *Raeta meridionalis* TATE. Right: Figures 5 - 9 of plate 25 of HEDLEY, 1900, which he also identified as *Raeta meridionalis* TATE.

The problem is further confused by the account HEDLEY (1900) gave of  $1\frac{1}{2}$  additional specimens which he found. Although his shells were reported to be authenticated by TATE, the size, shape and sculpture all suggest a species of the *Raetella pulchella* group. The peculiar drawing of the sculpture also suggests the concentric undulations are slightly oblique to the lines of growth, as in *Raetella*, and not vermiculate textural features characteristic of *Raeta* and *Raetina*. HEDLEY's remarks and figures are here reproduced (Figure 20, right).

"This species has hitherto been known from a single valve found on the beach of Aldinga Bay, South Australia. This year I have taken a whole shell containing part of the animal, and on another occasion a broken valve on "Chinaman's Beach", Middle Harbour. Prof. Tate, to whom one valve was submitted, kindly informs me that there is no essential difference between it and the type of *meridionalis*. My specimens are smaller, being 28 mm in length and 21 mm in height. Being perfect, I have utilized my example to draw the valves in apposition and other details not obtainable from the single valve hitherto known.

"Though disagreeing by vermiculate sculpture, the species seems to me nearer to the subgenus *Raetella*, DALL, than to any other division of *Labiosa*."

Possibly there are two species along the shore of southern Australia, one described by HEDLEY being similar to *Raetella pulchella*, the other to a sub-oval *Raeta* (*Raetina*) *pellicula*. SMITH (1914, p. 150) cites *Cypricia grayi* H. ADAMS (which is *Raeta grayi* H. ADAMS cited above in the synonymy of *Raeta pellicula*) from Queensland, Australia, and notes a reference which I have not seen, which does the same (HEDLEY, 1910, Rep. Austral. Assoc. Adv. Sci. for 1909, p. 351).

NICKLÈS (1950, p. 209) cites a "*Labiosa vitrea* GRAY" from the west coast of Africa ("Casamance à la Guinée française; Congo français"), with a brief description and figure. The general shape is that of *Raetella*, but the size is larger (up to 50 mm long). There are regular undulations only on the posterior slope, which is unusual for this genus. This is possibly *Mactra vitrea* GRAY, 1837 (Charlesworth's Mag. Nat. Hist., New Ser., vol. 1, p. 372, not figured) described from unknown locality. LAMY (1917, pp. 273 - 274) placed this in the subgenus *Mactrinula* of *Mactra*, but did not figure or describe it, nor did he know the locality of the material which he examined in the Paris Museum. I have seen no specimens, and cannot comment on its possible membership in *Anatina* or *Raeta*.

As LAMY (1917) has noted, *Raeta lyrata* "HINDS Ms." H. & A. ADAMS (1856) is a nomen nudum, and *Raeta bracheon* STURANY, 1899 (p. 12; pl. 3, figs. 1 - 6; Gulf of Suez, 50 fathoms) belongs elsewhere. LAMY says it is *Leptomya cochlearis* HINDS, of the Scrobiculariidae.

The *Raeta tenera* "DESHAYES" listed by H. & A. ADAMS possibly refers to "*Mactra tenera* Desh." listed as a synonym of *Mactra anatinoides*, with query, by REEVE. AS TOMLIN (1924) implies, no such species seems to have been described by DESHAYES.

According to the Zoological Record, LI (1930) described a new species, *Raeta maxima*, but I have been unable to locate that article.



## SYSTEMATIC DISCUSSION

Much essential information relevant to the phylogeny and life habits of this group is likely to be gained by further investigation of their anatomies. There are also characters of the shell which have not been given adequate attention. Admittedly, the species of this review were chiefly considered on the basis of those traditionally grouped together. Anatomical studies on these and other mastrid species may well indicate revisions of the classification quite different from that proposed by DALL (1895, 1898) and expanded by LAMY (1917). Several examples of shell characters whose significance is unexplored occurred to me during the present study. One is that thin-shelled mastrids generally have corrugated concentric sculpture, with the ridges affecting both the inner and outer shell surface, as in *Raeta* and *Raetella*, or they have a keel along the post-dorsal slope as in *Anatina*, *Mactra alata*, and *M. fragilis*; this keel I have called a corcelet, although aware that it may not be homologous to structures so named in other families. Perhaps the corrugations and keel are devices which strengthen the shell. In some species both are present, notably *Harvella elegans* from the tropical part of the western shores of the Americas. *Mactra iheringi* (DALL, 1897), from the east coast of South America, is very similar to *H. elegans* in size, shape and dentition, but it is a much thicker shell, with smooth external surface and no corrugations or post-dorsal ridge. That these two represent analogous species on the two sides of the continent should be given further study.

Incidentally, *Harvella elegans* seems to have vermiculate texture similar to that of *Raeta plicatella*, and the distribution of this feature among thin-shelled mastrids with corrugated shells should be studied.

In a rare species of the Indo-Pacific, *Mactra (Mactrinula) plicataria* LINNAEUS, 1767, the front end of the shell is disproportionately elongate, with the hind end truncated, and a form recalling *Donax*. This genus has further developed a thin shell, with corrugate sculpture and vermiculate texture very similar to *Raeta*. The disk, however, is not exceptionally swollen.

In the group of *Anatina*, *Raeta*, and *Raetella* there is a more pronounced swelling of the disk, which is not medial, but extends more toward the front end of the shell. In its extreme form, such as found in *Raeta* s. s., a shape recalling that of *Cuspidaria* results. This is just the opposite of the disk swollen along a line running postero-ventrally such as found in the Mytilidae and Carditidae.

*Raetella* may be no more closely related to *Raeta* and *Raetina* than any of them are to *Harvella* or *Mactrinula*. The sculpture of *Raetella* recalls that of the West American *Tumbeziconcha*, which, however, has the posterior

end of the shell extended, and the obliquity of the ridges on that end, rather than on the front one.

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